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Persistent shift of *Calanus* spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate

Inga Kristiansen[1]*, Eilif Gaard[1], Hjálmar Hátún[1], Sigrún Jónasdóttir[2], and A. Sofia A. Ferreira[2]

[1]*Faroe Marine Research Institute, Nóatún 1, PO Box 3051, Tórshavn FO-100, Faroe Islands*
[2]*National Institute of Aquatic Resources, Technical University of Denmark, Jægersborg Allé 1, Charlottenlund DK 2920, Denmark*

**Corresponding author: tel: + 298 353900; fax: + 298 353901; e-mail: ingak@hav.fo*

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The southwestern Norwegian Sea is characterized by an inflow of warm and saline Atlantic water from the southwest and cold and less saline East Icelandic Water (EIW), of Arctic origin, from the northwest. These two water masses meet and form the Iceland-Faroe Front (IFF). In this region, the copepod *Calanus finmarchicus* plays a key role in the pelagic ecosystem. Time-series of *C. finmarchicus* and *Calanus hyperboreus* in May and September, extending back to the early 1990s, were studied in relation to phytoplankton bloom dynamics and hydrography. The main reproductive period of *C. finmarchicus* started consistently earlier south of the IFF, resulting in different life cycles and stage compositions in the two water masses. In 2003, a sudden shift occurred north of the IFF, resulting in a similar phenology pattern to south of the IFF. Before this, only one generation of *C. finmarchicus* was produced in the Arctic water, but the earlier reproduction enabled the species to produce two generations after 2003. Simultaneously, *C. hyperboreus*, an expatriate in the EIW, largely disappeared. Food availability is unlikely the reason for the phenological differences observed across the front, as the typical pattern of the phytoplankton spring bloom showed an earlier onset north of the IFF. Temperature and salinity peaked at record high values in 2003 and 2004, and therefore possible links to oceanography are discussed. The dominant role of *Calanus* spp. and the potential linkages to water mass exchanges may herald strong effects on the ecosystem and pelagic fish in this subpolar Atlantic region under expected climate change.

Keywords: Atlantic water, *Calanus finmarchicus*, *Calanus hyperboreus*, East Icelandic Water, phenology, population dynamics, southwestern Norwegian sea, time-series.

Introduction

Modified North Atlantic Water (MNAW) (Hansen and Østerhus, 2000), hereafter termed Atlantic Water or simply AW, flows into the Norwegian Sea in the southeast (Mork *et al.*, 2014). This water mass has warmed markedly after the mid-1990s, partly due to a westward retraction of the Subpolar Gyre and an associated increased influx of warm subtropical waters. (Hátún *et al.*, 2005; Larsen *et al.*, 2012; Mork *et al.*, 2014). Studies within this area and elsewhere have shown that temperature changes and shifts in water masses can affect the biogeographical range and phenology, i.e. seasonal timing of zooplankton (Beaugrand and Reid, 2003; Edwards and Richardson, 2004; Hátún *et al.*, 2009; Ji *et al.*, 2012).

The Norwegian Sea is influenced by poleward flow of warm and saline AW, which enters in the southeastern region (Figure 1b). As it continues northwards, the water becomes cooler, fresher, and denser. A fraction recirculates in the Norwegian Basin and flows southwards, along the Jan Mayen Ridge, towards the Faroe Islands as the Recirculated Faroe Current (RFC; Hansen and Østerhus, 2000). The water from this flow eventually becomes submerged underneath the upper layer as cooled and freshened Norwegian North Atlantic Water (NNAW; Figure 1b; Read and Pollard, 1992).

From the Iceland Sea, the East Icelandic Current (EIC) transports cold East Icelandic Water (EIW) southeastwards where it meets the warmer and more saline AW in the southwestern Norwegian Sea. This encounter establishes the dynamic Iceland-Faroe Front (IFF). Below the surface, the IFF slopes downwards towards the south and west until it intersects the bottom on the top of the Iceland-Faroe Ridge (IFR) and along the northern Faroe slope at depths of 400–500 m (Hansen and Østerhus, 2000). At larger depths north of the ridge, fairly homogeneous water of Arctic origin dominates (Figure 2).

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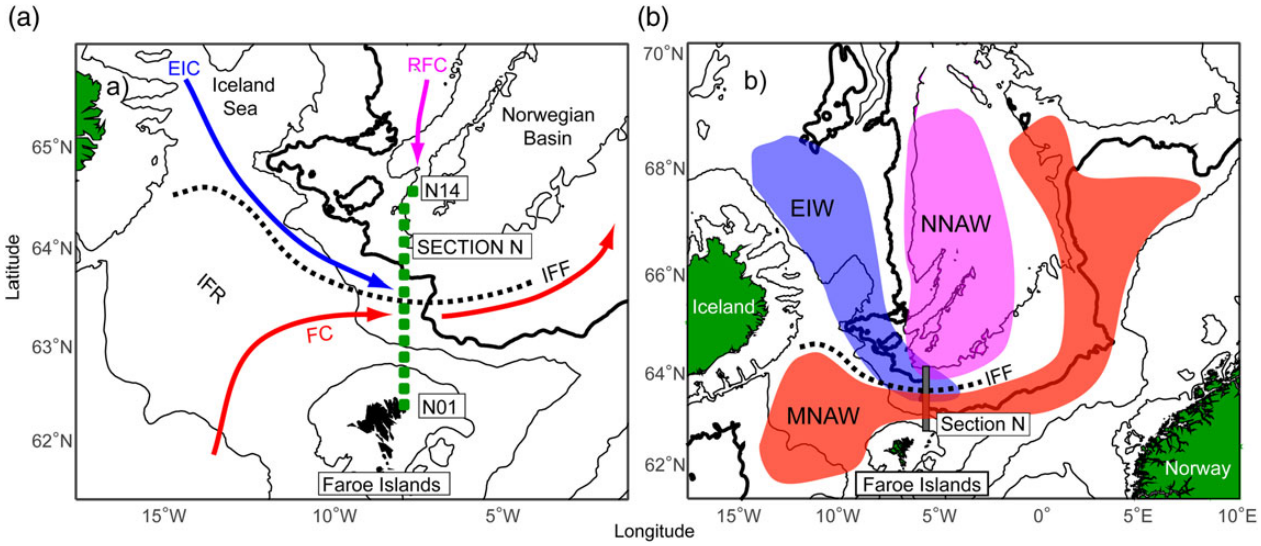

Figure 1. Map of the study area. (a) Main currents and Section N and (b) distribution of associated water masses. Abbreviations: FC, Faroe Current; RFC, Recirculated Faroe Current; EIC, East Icelandic Current; MNAW, Modified North Atlantic Water; EIW, East Icelandic Water; NNAW, Norwegian North Atlantic Water; IFF, Iceland-Faroe Front; IFR, Iceland-Faroe Ridge; JMR, Jan Mayen Ridge. The green dots in (a) and the thick grey line in (b) north of the Faroe Islands display the sampling sites (Section N). The 200, 500, 2000 (bold), and 3000 m isobaths are shown.

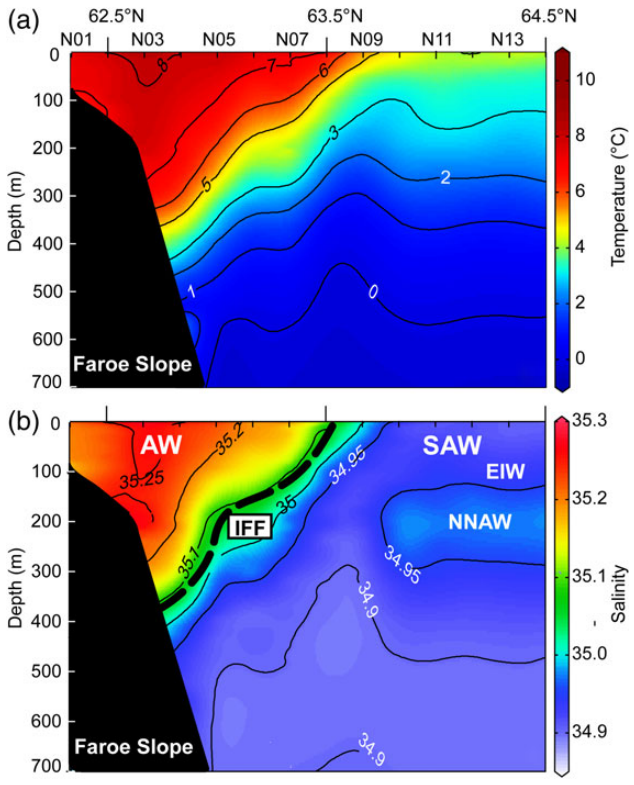

Figure 2. Average temperature (a) and salinity (b) along Section N. Averages are for February and May at each station from 1993 to 2013. The Iceland-Faroe Front (IFF) is defined between the 35 and 35.1 isohaline.

In the Norwegian Sea, the dominating zooplankton in terms of biomass is copepods of the genus *Calanus* where *Calanus finmarchicus* is the most abundant species. *Calanus finmarchicus* co-occurs with its sibling species *Calanus hyperboreus*, particularly in the cold water masses in the western region of the Norwegian Sea (Wiborg, 1955; Broms *et al.*, 2009). *C. finmarchicus* is the main secondary producer in the North Atlantic ecosystem (Stenevik *et al.*, 2007) and several commercially important fish stocks rely on this lipid-rich species as a main food source (Prokopchuk and Sentyabov, 2006; Broms *et al.*, 2012; Debes *et al.*, 2012). *C. hyperboreus* is also of ecological importance, particularly in the cold water, both as a grazer and as a food item for pelagic fish, fish larvae, birds, and marine mammals (Baumgartner and Mate, 2003; Dahl *et al.*, 2003; Berge *et al.*, 2012).

The Norwegian Basin is one of the main centres of abundance for overwintering populations of *C. finmarchicus* (Melle *et al.*, 2014). In late summer, *C. finmarchicus* descends (usually as copepodite stage IV or V) to depths between 500 and 1200 m (Heath *et al.*, 2000a) where a phase of low metabolic activity ensues. The deep part of the Norwegian Sea is characterized by a cyclonic gyre, which is steered by bottom topography (Jakobsen *et al.*, 2003) and plays a critical role in retaining the animals within the basin, while residing at great depth (Melle *et al.*, 2014). North of the Faroe Islands, RAFOS floats (Rossby *et al.*, 1986) have revealed very slow deep currents (Søiland and Huse, 2012), which advect a part of the overwintering population through the Faroe-Shetland Channel southeast of the Faroe Islands (Heath and Jónasdóttir, 1999; Heath *et al.*, 2004).

The overwintering animals (G_0) start their ascent towards the upper layers in late winter and early spring where they moult and reproduce (Heath and Jónasdóttir, 1999; Gaard and Hansen, 2000; Hirche *et al.*, 2001). The initial phase is likely supported by internal wax-ester reserves (Jónasdóttir, 1999; Madsen *et al.*, 2008), while the main reproduction relies on ingested food and peaks with the phytoplankton bloom (Gaard, 2000; Heath *et al.*, 2000b; Debes *et al.*, 2008; Jónasdóttir *et al.*, 2008). By mid to late summer, individuals from the new generation (G_1) may continue into adulthood and produce a second generation (G_2) or retain their lipid storage, arrest their development, and descend into overwintering depths (Heath *et al.*, 2000b; Broms and Melle, 2007; Melle *et al.*, 2014).

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Calanus hyperboreus is of Arctic origin, with a main distribution in the Arctic Ocean, the Greenland, and Iceland Seas (Wiborg, 1955; Conover, 1988; Hirche, 1997). It is advected with the EIC into the southwestern Norwegian Sea. It has a similar life cycle to *C. finmarchicus*, however with a longer generation time that can take from 2 to 4 years to complete (Hirche, 1997).

In 1993, the Faroe Marine Research Institute (FAMRI) established a monitoring programme focusing on the state of the pelagic ecosystem north of the Faroe Islands, along the so-called Section N (Figure 1). In the near-surface layer, it covers distinct water masses, separated by the IFF. Warm and saline AW occupies the southern part, while the cold and less saline EIW and NNAW, hereafter collectively termed Subarctic Water (SAW), characterize the northern domain of Section N. (Figure 2). This study introduces a time-series for *C. finmarchicus* and *C. hyperboreus* at Section N and links the population dynamics with phytoplankton availability and hydrography. Potential links to water mass redistributions and feeding conditions for the large pelagic fish stocks in the region are also discussed.

Material and methods

Location and sampling

Section N is comprised of 14 sampling stations (N01–N14) that extend northwards from the Faroe Islands and into the southwestern Norwegian Sea (Figure 1a). The stations are located equidistantly from 62°20′N to 64°30′N at longitude 6°05′W, except for station N14, which is located at longitude 6°00′W. The distance between stations is 10 nautical miles. Observations of hydrographic properties (temperature and salinity) started in 1988 and have typically been collected four times a year. In 1993, monitoring of zooplankton composition was initiated and has taken place in mid to late May to present date. In 1995, then more routinely in 2000 and onwards, zooplankton data were also collected in late August or early September, hereafter referred to as September. Additionally, sampling was also carried out on five occasions in 1995 to obtain an overview of seasonal variation. No zooplankton samples were collected in May 1996, 1998, 2006, or in September 2012.

Oceanic environment

Vertical profiles of temperature and salinity were obtained at each station with a CTD (Seabird Electronics 911 Plus) down to 1100 m. Salinity was calibrated against standard seawater with an Autosal 8400A salinometer. A fluorometer was mounted on the CTD, so fluorescence profiles were measured simultaneously with the hydrographic properties. Fluorescence values were calibrated against chlorophyll *a* samples, which were measured spectrophotometrically according to Parsons *et al.* (1984).

Zooplankton

Zooplankton samples were collected using a WP-2 net with a 200-μm mesh size and 0.25 m^2 mouth opening. The net was towed vertically from 50 m depth to the surface with a speed between 0.3 and 0.5 m s^{-1}. Zooplankton samples were preserved with 4% formaldehyde. In the laboratory, samples were divided into subsamples with a Motoda splitter. Subsamples contained at least 200 individuals. The animals were identified and counted, and *C. finmarchicus* were further classified into copepodite and adult stages. Since the 200-μm mesh net highly undersamples nauplii, these are not included in this study. Abundance (numbers per m^3) was calculated using the diameter of the net opening and the sampling depth.

Bloom initiation metric

Bloom initiation was estimated by using chlorophyll *a* concentration as a proxy for phytoplankton concentration. The chlorophyll *a* concentration product was downloaded from the European Node for Global Ocean Colour (GlobColour Project, "http://www.globcolour.info/"). This project merges data from three satellite sensors: SeaWiFS, MODIS-AQUA, and MERIS using the Garver-Siegel-Maritorena (GSM) algorithm (Maritorena *et al.*, 2002) to generate a merged, global ocean colour product. Daily data were used from 1998 to 2011 with a 4-km grid. Smoothing of each seasonal cycle was performed on the natural log-transformed data of chlorophyll *a* concentration with a generalized additive model using the software R, thus allowing for a gap-free dataset from the first observation of the year to the last. Bloom initiation was estimated by applying a 5% increase above the annual median (Siegel *et al.*, 2002) to the smoothed, non-log-transformed seasonal cycle of chlorophyll *a* concentration as shown in Ferreira *et al.* (2014). This metric has been widely used in the literature [see references in Ferreira *et al.* (2014)], which provides a fair comparison of results.

Data analysis

Section N was divided into two areas, defined by the distinct north-south salinity characteristics of the region. Stations with salinity values >35 and <35 psu were allocated to AW and SAW, respectively (Figure 2). As our interest was to investigate the zooplankton composition in the pure AW and SAW, stations located in the frontal region, which was defined according to the sharp drop in salinity, were excluded from the study. The number of stations in AW varied between three and seven and in the SAW between three and eight, depending on the location of the IFF during each cruise. Therefore, the data for the two different water masses are presented as average values for each year. The two southernmost stations (N01 and N02) are influenced by on-shelf water and are therefore also excluded in this study.

Time-series of temperature and salinity of the AW were determined according to methods described by Larsen *et al.* (2012). The position of the *AW core* was found based on maximum salinity. Centred on the maximum salinity, average values were calculated over a 50-m depth layer. The seasonal variation was estimated by monthly averages or by a fitted cosine when data coverage was too sparse. The presented deseasoned time-series were calculated by subtracting the seasonal variation from the original values.

For the bloom initiation metric, 7°W–5.2°W, 62.8°N–63.2°N was selected to represent the AW and 7°W–5.2°W, 64°N–64.4°N to represent the Arctic water north of the IFF.

Results

Hydrography

The 20-year average temperature and salinity distributions on Section N (Figure 2) show the AW as a warm and saline wedge-shaped region in the southernmost part over the Faroe slope. The AW is bounded at its northern side by the IFF, most clearly identified by the salinity distribution. North of the IFF, the colder and less saline SAW characterize the region.

After a record low temperature of 7°C in 1995, the temperature of the AW has been rising (Figure 3). From 2002 to 2003, the

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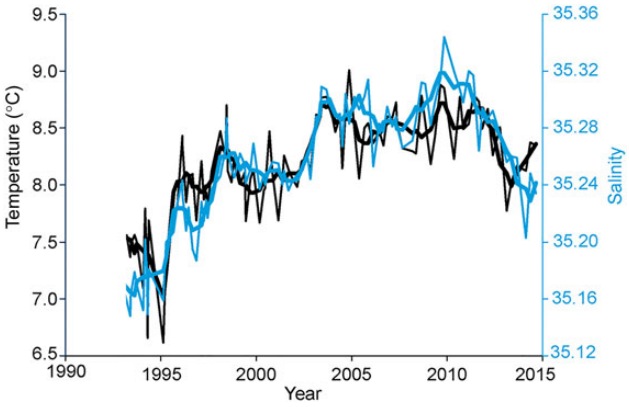

Figure 3. Atlantic Water (AW) temperature (black) and salinity (blue) averaged over a 50-m depth layer (see the section "Data analysis") at Section N. The thin lines are measured values, whereas the thick lines show a 1-year running mean of deseasoned values.

temperature of the *Atlantic core* sharply increased from ~8.0 to 8.6°C. Subsequently, it levelled off with no consistent pattern until 2011–2013, when it started to decrease again towards 8°C. However, the last two years indicate an upward trend. The salinity varied in parallel with temperature, with an overall increase of ~0.15 psu from 1995 to 2009.

Throughout the sampling period, the frontal region did not extend farther north than station N09. Thus, stations N10 to N14 purely represent SAW. The average values for temperature and salinity of various depth layers are displayed in Figure 4. The upper 150-m layer showed a fluctuating, yet increasing trend in temperature. Similar to the AW, the SAW temperature sharply increased ~1°C in 2003, from 3.8 to 4.7°C. A year later, the temperature peaked at 4.9°C. Subsequently, it decreased again, fluctuating between 3.8 and 4.7°C. This pattern is also seen at other depth intervals, but with less variability. Overall, the salinity in the SAW displayed an increasing trend, with less fluctuation at greater depths. Salinity in the upper 150 m showed greatest variability, with a sharp decrease in 1997, followed by a sharp increase in 2003.

Calanus spp. distribution, abundance, and stage composition

Seasonal development of C. finmarchicus

The seasonal variation in *C. finmarchicus* dynamics at Section N, sampled in 1995, is displayed in Figure 5. In February, the G_0, consisting of stage CIV and CV, had not arrived to the upper 50 m. By April, the abundance of G_0 had increased in the surface layer in both water masses and had started to moult into adults (CVI). However, the proportion of adults was markedly higher in the AW than in the SAW. In May, the population had further increased on both sides of the IFF. G_1, consisting of CI–CIII, had appeared and was dominating in the AW (Figure 5b), while the population in the SAW was still mainly composed G_0 and CVI (Figure 5a). In September, CIV and CV, which probably belong to G_1, were dominating in the SAW while a fraction of younger copepodites, most likely originating from a G_2, were present in the AW. In October, the animals had largely disappeared from the surface waters.

Interannual variations of C. finmarchicus

The zooplankton time-series at Section N covers 18 years of observations in May, starting in 1993 and 15 years in September, starting

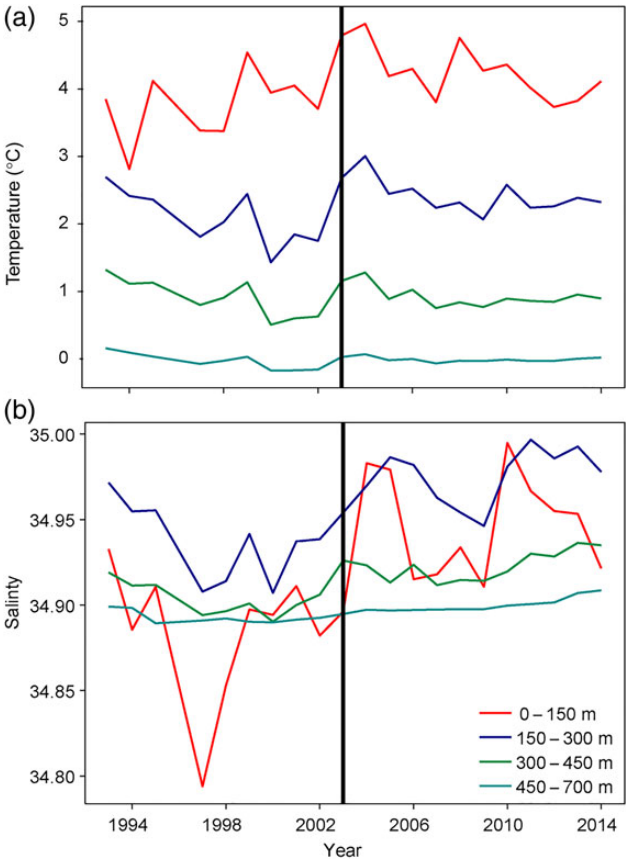

Figure 4. Variation in temperature (a) and salinity (b) from 1993 to 2014 in the Subarctic Water (SAW) at Section N. Averages from February and May from station N10–N14 at 0–150 m, 150–300 m, 300–450 m and 450–700 m are shown. The year of the phenological shift (2003) is emphasized with the vertical line.

in 1995. Throughout the entire May sampling period, the numbers of *C. finmarchicus* in the AW were dominated by CI–CIII, while the numbers of CIV–CVI were significantly lower (Figure 6b). On the other hand, in the SAW, the G_0 and those individuals that had moulted into adults were dominating. Very few young copepodite stages occurred before 2003 (Figure 6a). Hence, the reproduction in the SAW likely started significantly later than in the warm AW. The small amount of CI–CIII present north of the IFF indicates that the onset of reproduction in the SAW only started shortly before the sampling. In 2003, a significant reduction of CIV–CVI and an increase of CI–CIII occurred in May in the SAW (Figure 6a and c). This phenology shift has been persistent since 2003 and mirrors now the reproductive pattern in the AW, south of the IFF (Figure 6b and d).

Although fluctuating, the mean abundance of CI–CIII in the SAW has gradually increased after the phenological shift and became record high in 2014 (Figure 6a). However, overall it has remained lower compared with the number of *C. finmarchicus* individuals south of the IFF (Figure 6b). Apart from a few years, the proportion of CI–CIII, CIV–CV, and CVI in the AW has remained quite stable throughout the sampling period, with CI–CIII comprising over 70% of the population (Figure 6d). On the other hand, the population in the SAW was comprised of ~80% of the G_0 and CVI (Figure 6c). After 2003, the relative abundance in May became similar to the population composition in the AW.

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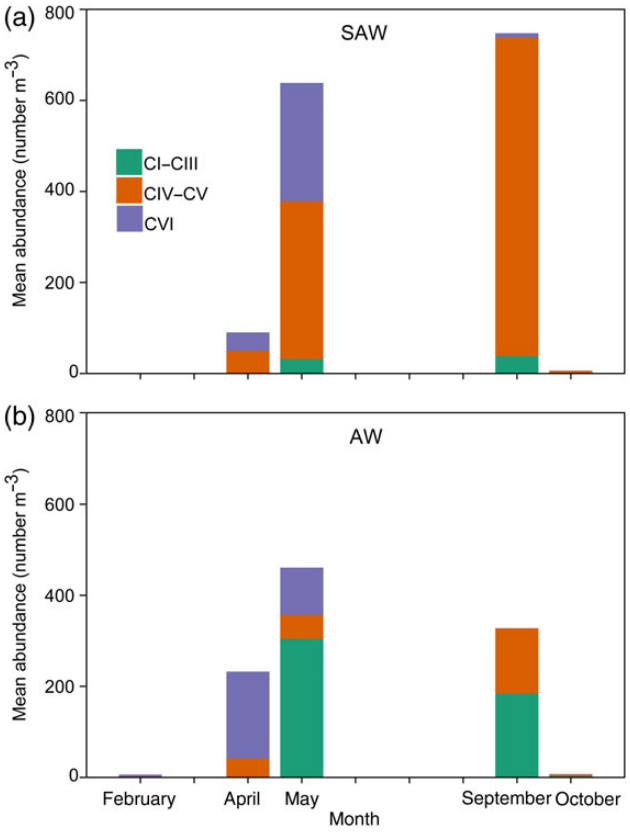

Figure 5. Seasonal variation of *Calanus finmarchicus* in the upper 50 m in 1995 in the (a) Subarctic Water (SAW) and (b) Atlantic Water (AW) at Section N.

In September, the abundance was around four times higher in the SAW compared with the AW (Figure 6e and f), consisting of approximately 1000 individuals m^{-3} and 200–300 individuals m^{-3}, respectively. An increasing amount of young copepodite stages, which most likely belonged to G_2, were recorded after the phenological shift in the SAW domain along Section N.

Interannual variations of C. hyperboreus

Before 2003, *C. hyperboreus* used to be a common species in the zooplankton community, especially in the SAW where the abundance was ~10 times higher than in the AW in May (Figure 7). Although the developmental stages were not routinely noted, individuals commonly observed consisted of CIV, CV, and CVI. Stage CIII was only occasionally recorded. However, since 2003, *C. hyperboreus* largely disappeared. Only a marginal number of individuals were recorded in September.

Phytoplankton

Analysis of chlorophyll *a* estimates from satellite observations showed that the timing of the spring bloom onset can be grouped into two distinct regions, bounded by a line which roughly follows the IFF (Figure 8a). Time-series extracted to represent the AW (black box) and SAW (white box) (Figure 8a), showed a distinct pattern. The seasonal timing of the spring bloom onset generally occurred earlier in the SAW, ranging from day 105 to 136, and later in the AW, ranging from day 145 to 160 (Figure 8b). Although fluctuating, the water masses generally showed opposite trends in bloom dynamics: when the onset of the bloom occurred earlier in the SAW, the bloom was further delayed in the AW. The strongest opposite pattern in the water masses was observed in 2003.

The *in situ* concentrations of chlorophyll *a* in May (obtained concurrently with the zooplankton samplings) showed that the mean phytoplankton biomass in the upper 100 m was typically higher in the SAW compared with the AW, with an average chlorophyll *a* of 1.02 and 0.80 μg l^{-1}, respectively (Figure 9).

Discussion

Calanus abundance

The majority of the *C. finmarchicus* population at Section N is presumed to originate from the overwintering population within the Norwegian Basin. A seasonal basin scale study conducted by Bagøien *et al.* (2012) showed that there was no difference in the abundance of *C. finmarchicus* between Atlantic and Arctic water from 1993 to 2008 in the Norwegian Sea. In contrast, Broms *et al.* (2009) recorded a higher abundance in the Atlantic water. At Section N, the abundance of *C. finmarchicus* in May, mainly consisting of the earlier occurrence of CI–CIII, was approximately twice as high in the AW compared with the SAW before 2003 (Figure 6a and b). Although fluctuating, the mean abundance in the SAW has been gradually increasing after 2003 and became record high in 2014, due to the increasing number of G_1. However, overall it has remained lower compared with the population in the AW. Broms and Melle (2007) hypothesized that recruitment of *C. finmarchicus* in the SAW is less successful due to delayed reproduction compared with the phytoplankton bloom. This mismatch may reduce survival and reproductive success, and thus lower the abundance. However, at Section N, we see that the onset of the phytoplankton bloom occurs earlier in the SAW (Figure 8). Thus, the lower temperature in the upper layer in the SAW, ranging ~4°C compared with ~8°C in the AW, is more likely to place a restriction on the development rates rather than the phytoplankton production. According to Campbell *et al.* (2001), this temperature difference prolongs the duration from egg to CV between 20–30 d in the SAW. In September, the lower abundance in the AW suggests that the *C. finmarchicus* population have started to descend from the surface water before the population in the SAW (Figure 6e and f). This is most likely because they reach the overwintering stages quicker with sufficient lipid content, making them ready for dormancy (Jónasdóttir, 1999; Irigoien, 2004).

Calanus hyperboreus has a centre of abundance in the Greenland Sea (Conover, 1988; Hirche, 1997), with a possible connection to the stocks in the northern part of the Iceland Sea (Astthorsson and Gislason, 2003). Most likely, the individuals found in this study have, to a large extent, been advected with the EIC towards Section N (Wiborg, 1955). Consequently, the abundance is much higher north of the IFF compared with the south (Figure 7). Thus, the few individuals recorded south of the IFF are likely to originate from the EIW that has been submerged in the frontal zone and advected southeastwards below the AW (Figure 1b; Read and Pollard, 1992). The submerged water mass contains overwintering populations that may eventually ascend into the overlying AW (Melle *et al.*, 2004; Broms *et al.*, 2009). By August, *C. hyperboreus* have largely disappeared from the upper layer in the Iceland Sea (Astthorsson and Gislason, 2003). This is consistent with our results from Section N that has only had four individuals recorded in the September time-series from 1993 to 2014 (not shown).

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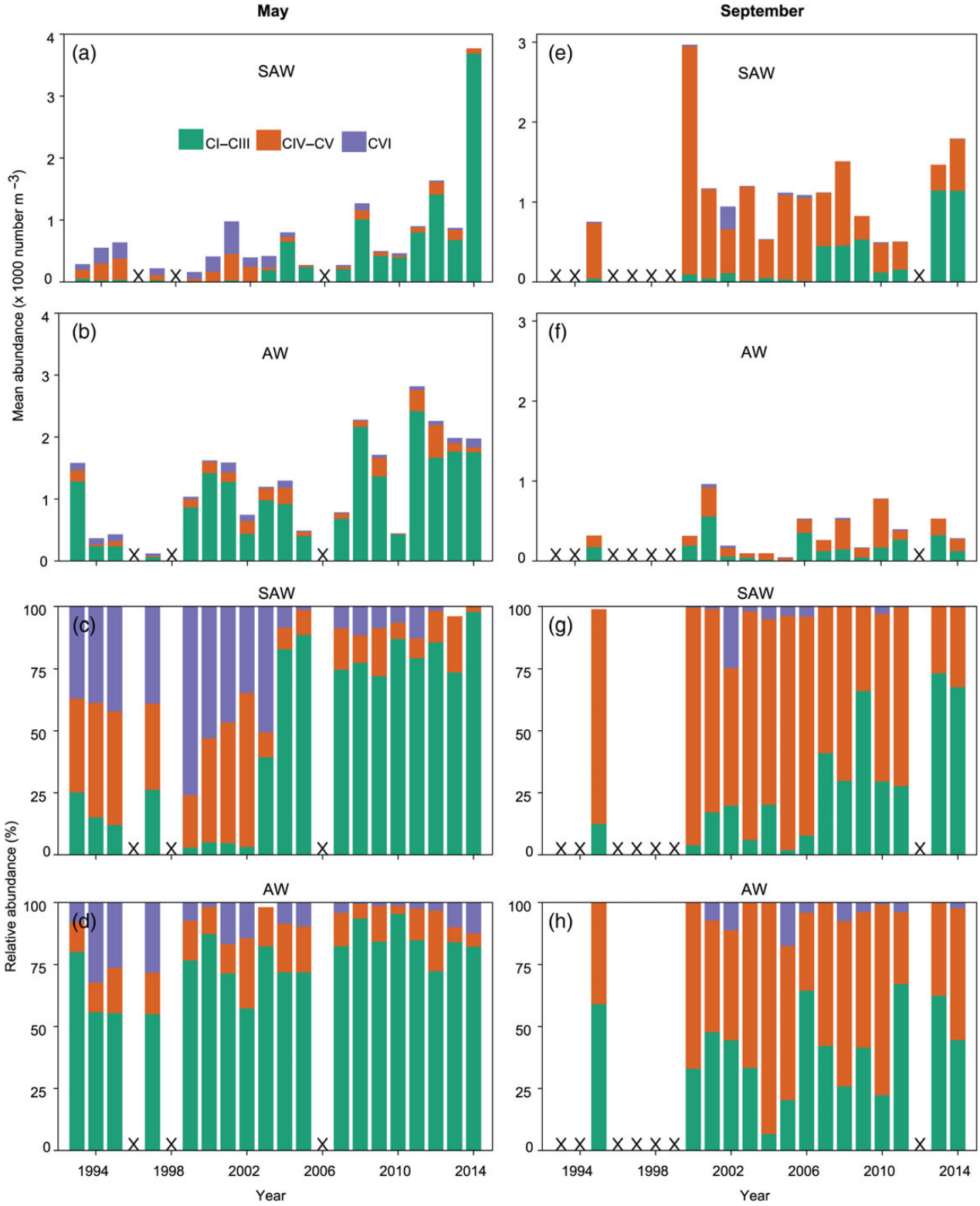

Figure 6. Interannual variations in the mean abundance (numbers m^{-3}) and relative abundance of *Calanus finmarchicus* developmental stages in May (left) and September (right), in Atlantic Water (AW) and Subarctic Water (SAW) at Section N. Absolute abundance is displayed in the upper panels (a, b, e, and f), and relative abundance in the lower panels (c, d, g, and h). Years with missing data are indicated by crosses.

Shift in reproduction phenology of *C. finmarchicus*

Gaard and Nattestad (2002) have previously reported that the earlier gonad maturity and onset of reproduction of *C. finmarchicus* at Section N in the AW, compared with the SAW, is linked to more mature females. This was reflected in the dominance of G_1 in the AW while the population in the SAW mainly contained G_0

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individuals in May (Figure 6a and b respectively). However, since 2003, the onset of reproduction in the SAW has likely occurred earlier compared with the previous 10 years and is mirroring the reproduction pattern in the AW. Therefore, the phenological changes indicate that the females present in the SAW after 2003 reach maturity earlier and are thus able to initiate earlier reproduction. Although most G_1 individuals migrate downwards to dormancy when reaching CIV or CV in midsummer, some individuals tend to remain in the upper layer to produce a G_2 (Figure 6e and g). This was not possible or successful before 2003 as the G_1 reached stage CIV and CV later in summer. However, in recent years, the increasing number of CI–CIII in September in the SAW must be assumed to belong to a G_2. Thus, the phenological shift also seems to have increased the secondary production in the SAW.

As illustrated in Figure 6c, the shift in phenology has been persistent and comparable to a shift between two different regimes. This is likely to have large consequences for higher trophic levels, including commercially important pelagic fish species. Therefore, it is important to understand the mechanisms behind these changes. The observed phenology shift may be caused by alterations in the local conditions, primarily food (phytoplankton) availability or temperature. Another possibility is a change in advection of the EIW. We discuss these possibilities, together with the disappearance of *C. hyperboreus*, separately in the following sections.

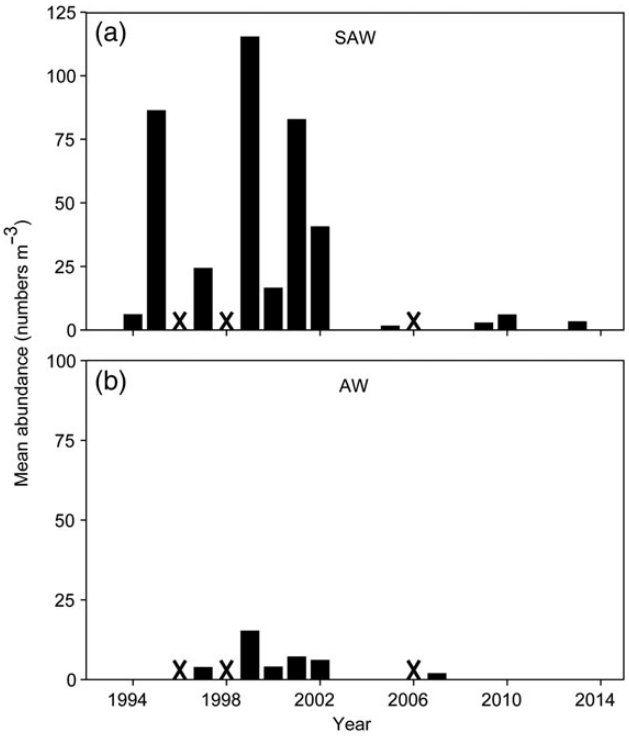

Figure 7. Mean abundance of *Calanus hyperboreus* in the (a) Subarctic Water (SAW) and (b) Atlantic Water (AW) in May from 1993 to 2014. Years with missing data are indicated by crosses.

The phenology shift in relation to the phytoplankton bloom

The typical temperature in the upper layer in the AW and SAW in spring is, as mentioned, ~8 and 4°C, respectively. At these temperatures, stage duration from spawning to CI can be estimated to 3 weeks in the AW and 4 weeks in the SAW (Campbell *et al.*, 2001). Thus, stages CI–CIII in May (Figure 6) are spawned around late April, which is during the pre-bloom rather than the bloom period itself. Reproduction of *C. finmarchicus* is closely linked to the seasonal development of the spring bloom (e.g. Heath *et al.*, 2000b, and references therein). Although the fecundity is largely dependent on food availability, there is also a significant egg production during the pre-bloom period (Niehoff *et al.*, 1999; Stenevik *et al.*, 2007), which is thought to be mainly fuelled by lipid reserves (Madsen *et al.*, 2008). In contrast to the observations by Broms and Melle (2007), we see in Figure 8 that the onset of the phytoplankton bloom occurred earlier in the SAW and later in the AW. In addition, the *in situ* chlorophyll *a* measurements in May (Figure 9) showed a higher phytoplankton biomass north of the IFF, apart from two years. This regional difference is caused by earlier stratification, which is induced by a low saline upper layer in the SAW (Zhai *et al.*, 2011). Despite these apparent good feeding conditions, gonad maturity, and thus reproduction, was impeded in the SAW before 2003 (Gaard and Nattestad, 2002). Primary production

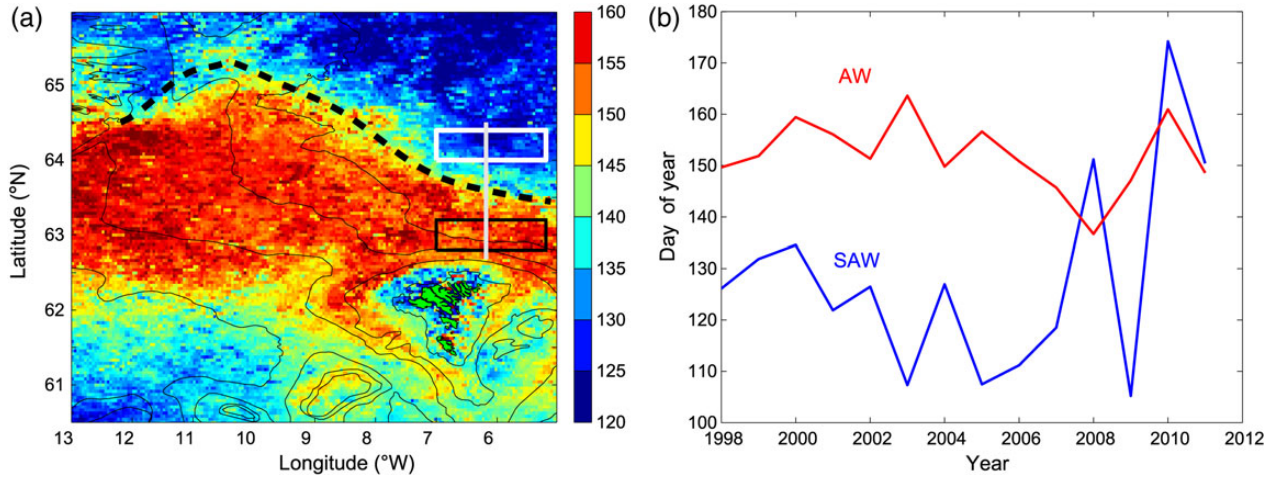

Figure 8. Onset of the spring bloom from 1998 to 2011. (a) Average time (day number) of the bloom initiation and (b) associated time-series of average day number of the bloom onset for each year in the Atlantic Water (AW, red line) and Subarctic Water (SAW, blue line). The values in (b) have been extracted from the boxes shown in (a). The dashed line illustrates the Iceland-Faroe Front (IFF).

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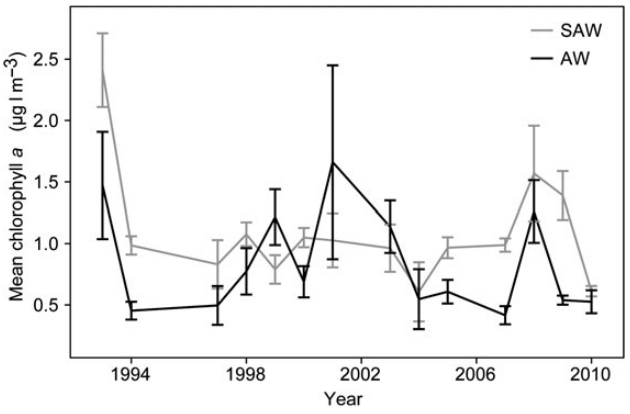

Figure 9. Mean phytoplankton biomass between 10 and 100 m depth in May from 1993 to 2010. The Atlantic Water (AW) represents stations N03–N05 and the Subarctic Water (SAW) represents stations N10–N14 (see Figure 2). The vertical lines show standard error, calculated from three and five stations in the AW and SAW, respectively.

is necessary for *C. finmarchicus* to have a successful recruitment rate, but the phytoplankton trend in the SAW did not show a pattern that supports the phenological shift. Therefore, we argue that the food conditions were not the main driving mechanism behind the later onset of reproduction in the SAW.

Potential links to ocean climate

Warming and salinification in 2003

Changes in zooplankton timing are strongly related to water masses and temperature (Ji *et al.*, 2010; Mackas and Beaugrand, 2010). The sudden phenological shift in reproduction (Figure 6a) and the sudden reduction in *C. hyperboreus* abundance, particularly in the SAW (Figure 7a), coincide with a marked shift in the hydrography. Our time-series shows that the temperature in the AW has been gradually increasing since 1995 (Figure 3). By 2002, the temperature had increased ∼1°C and in 2003, the temperature further increased 0.5°C compared with the previous year. The salinity varied in parallel with the temperature trend. According to Larsen *et al.* (2012), these changes were caused by advection of the warmer inflowing AW that are associated with the circulation strength and extent of the Subpolar Gyre, represented by a so-called gyre index (Häkkinen and Rhines, 2004; Hátún *et al.*, 2005). The gyre circulation was particularly weak in 2003, allowing an increased flow of unusually warm subtropical water merging with the Atlantic inflow that is carried into the Norwegian Sea. In addition to the warming Atlantic inflow, Hansen *et al.* (2015) has documented a sharp increase in volume and heat transport through Section N in 2003, which has remained higher compared with previous years.

Other hydrographic time-series in the Norwegian Sea also show an increasing trend in temperature and salinity (Drange *et al.*, 2005; Holliday *et al.*, 2008; Richter and Maus, 2011). At Ocean Weather Ship M (OWSM), located in the central Norwegian Sea, the same temperature trends were recorded around 2003, along with a sharp peak in salinity (Drange *et al.*, 2005). This is similar to the covariation seen between the hydrographic properties of the Atlantic inflow and OWSM, discussed by Holliday *et al.* (2008).

The rise in temperature will affect the NNAW, which the RFC transports south towards the northern part of Section N (Figure 1a), although air–sea heat exchange may modify this. In addition, the inflow of relatively cold and fresh EIW from the EIC may also vary (Blindheim *et al.*, 2000; Mork *et al.*, 2014).

Despite these potential modifications, we do see a marked temperature increase of ∼1°C around 2003 in the SAW (Figure 4) and the peak temperature at 4.9°C was reached the following year. According to the temperature-dependent developmental rates given by Campbell *et al.* (2001), a temperature increase by 0.5–1°C is, however, only expected to shorten the developmental rates in the SAW by 3–6 d. Thus, despite the sudden warming in 2003, faster developmental rates are not sufficient to support the hypothesis as a key mechanism behind the phenological change. It is, however, at present an unanswered question whether the temperature increase may have affected an earlier gonad maturity in the SAW.

In the Gulf of Maine, *C. hyperboreus* is found within a temperature range of 2–8°C (Conover and Corner, 1968). Therefore, it seems unlikely that the sudden reduction in *C. hyperboreus* in the SAW since 2003 is caused by the temperature increase from 3.8 to 4.7°C.

After the temperature peak in 2004, it decreased again, varying between 3.8 and 4.7°C. However, the changes in the *Calanus* spp. population in the SAW have persisted since 2003. Thus, the shift observed is comparable to a regime shift that has changed from one stable state to another as a non-linear response to an abrupt physical change as discussed by Hare and Mantua (2000) and Richardson (2008).

Circulation changes

Both *Calanus* species use the water column for their semi-annual vertical migration to enter and exit their diapause phase, which is typically reached at depths >500 m. During diapause, the deep water current controls the distribution of the animals (Søiland and Huse, 2012). Likewise, during ascent, the distribution is determined by the current system between deep water and surface water. Thus, any changes to these flow patterns can alter the origin and the extent of the organisms advected towards Section N. *C. hyperboreus* is of Arctic origin (Wiborg, 1955; Hirche, 1997; Asthorsson and Gislason, 2003) and therefore assumed to be advected in larger quantities with the EIW to the northern part of Section N rather than with the RFC. No data are available that can reveal whether the abundance of *C. hyperboreus* in the source region north and east of Iceland has decreased. However, the sudden co-occurring reduction in the abundance of *C. hyperboreus* and the phenology shift of *C. finmarchicus* towards earlier maturation and reproduction suggest that a proportion of the overwintering *C. finmarchicus* stock were advected with the same water mass as its congeneric species. These changes indicate that the deeper layer of the EIW (Figure 1b), which the overwintering stock of the *Calanus* species inhabits, has reduced its eastward extension into the study area after 2002. This has resulted in a dominance of individuals that originate from the Norwegian Basin in the SAW domain at Section N. Together with the reduced abundance of *C. hyperboreus*, which suppresses recruitment success of *C. finmarchicus* (Melle *et al.*, 2014), we see an increase of CI–CIII recruits.

Variability in the posture of the IFF, and thus in the thickness of the AW and the underlying EIW in the southern Norwegian Sea, induces change in the sea surface height (SSH) through the steric height relation—lower/higher SSH reflects more/less EIW (Hátún and McClimans, 2003; Richter *et al.*, 2012). This SSH variability is observed by satellite altimetry, and the first Empirical Orthogonal Function mode of SSH clearly identifies a broad band

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of elevated variability along the IFF, from Section N towards Norway (Richter *et al.*, 2012). The steric heights and altimetry derived SSH in the southern Norwegian Sea were record high in 2003 (Richter *et al.*, 2012), supporting our proposition of much reduced eastward influx of EIW this year. Reduced volume of EIW, and resulting increases in SSH, are, furthermore, associated with an anticyclonic windstress anomaly pattern over the southern part of the Nordic Seas (Blindheim *et al.*, 2000; Richter *et al.*, 2012).

A thorough test of this hypothesis is beyond the scope of the present work. Such a test would have to involve a comprehensive spatio-temporal satellite and hydrographic data collections, atmospheric forcing fields and preferably output from a realistic numerical ocean model, to complement and extrapolate, from the observations.

Potential consequences of the persistent *Calanus* shift for higher trophic levels

The Norwegian spring-spawning (NSS) herring is the first migrating stock to arrive in the Norwegian Sea. Its principal prey is *C. finmarchicus*, which it feeds on to build up its energy reserve after spawning (Debes *et al.*, 2012). During spring, the NSS herring adjust their migration pattern according to prey abundance of the overwintering stock: before a feeding area becomes depleted, the stock migrates to a different area with higher G_0 abundance. Later in the season when G_1 dominates, diet studies show less content in herring stomachs, which contain a wider variety of zooplankton type and size compared with the main feeding period in spring (Kaartvedt, 2000; Broms *et al.*, 2012). Due to its high biomass, *C. hyperboreus* is also an important energy source in the foodweb (Broms *et al.*, 2012), but due to its lower abundance compared with *C. finmarchicus* in the southwestern Norwegian Sea, more *C. finmarchicus* is detected in diet studies (Debes *et al.*, 2012). Mackerel arrives later than NSS herring to the Norwegian Sea, is less size selective and therefore mainly exploit the G_1, which is dominating upon their arrival in early summer (Kaartvedt, 2000).

The reduction of G_0 in May after the phenological shift in 2003 indicates poorer feeding conditions for herring, which prefer these larger individuals. To find suitable prey, the stock has to use more energy to migrate farther northwards (Prokopchuk and Sentyabov, 2006). Therefore, the energy transfer to higher trophic levels is likely to be most affected for the NSS herring. However, the earlier onset has prolonged the *C. finmarchicus* productive season in the SAW by initiating a G_2 production. Thus, food availability for mackerel might have both increased and been extended after 2003, suggesting that the area now can support a higher carrying capacity of mackerel.

Conclusions

Persistent changes since 2003 in the *Calanus* spp. populations north of the Iceland-Faroe Front in the southwestern Norwegian Sea are presented. The numbers of the younger stages in the *C. finmarchicus* population markedly increased, while the abundance of overwintering animals, sampled in May, decreased. Simultaneously, *C. hyperboreus* largely disappeared from Section N. No link was found to primary production, proxied by chlorophyll *a* concentrations, but the biological shift did coincide with an increase in temperature and salinity. The modest warming is, however, not deemed to have directly induced the biological shift, but it could be a reflection of more important water mass redistributions. We suggest that the changes in the *Calanus* spp. population dynamics may be caused by a westward retraction of the cold and low saline East Icelandic Water tongue. A potentially permanent reshaping of the water mass boundaries, induced by the expected climate changes, might therefore strongly impact the large pelagic fish stocks migrating to this region.

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